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IMMOBILIZATION OF THE PREDATORY GASTROPOD, *NUCELLA LAPILLUS*, BY ITS PREY, *MYTILUS EDULIS*

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ABSTRACT

Slow moving and sessile organisms cannot escape predators and must rely on other defenses. Laboratory experiments show that mussels (*Mytilus edulis*) immobilize predatory gastropods with byssal threads. This study assesses the risk of immobilization faced by the gastropod, *Nucella lapillus*, under natural conditions. Nearly 30% of the *N. lapillus* within mussel beds are trapped, and the per day risk to a predator in a mussel bed is between 0.010 and 0.038. The mussels nearest to the predator attach 20 or more byssi to the body whorl of its predator's shell. Byssi are retracted, flipping the predator over. *Nucella lapillus* are rarely found in mussel beds (0.10 individuals per 0.25 m^2 in beds and 2.38 per 0.25 m^2 out of beds). It is not clear if *N. lapillus* are avoiding mussel beds for other reasons, such as exposure to predators, or are seeking alternative prey which do not co-occur with mussels. Nevertheless, mussels pose a danger to predatory gastropods.

INTRODUCTION

Predation poses one of the greatest risks for slow-moving and sessile organisms and often limits the distribution of many such species (Connell, 1961; Paine, 1974; Menge, 1976; Vermeij, 1978; Peterson, 1979). While some clonal sessile marine invertebrates can survive partial destruction by predators (*e.g.* Harvell, 1984), non-clonal individuals must inhibit access by predators or live in areas where predators are otherwise excluded (Schmitt, 1981; Moran, 1985; Warren, 1985).

Mytilus is one of the most successful and ubiquitous genera on rocky shores and forms extensive beds that appear to be completely defenseless against predators. Other shelled marine invertebrates co-exist with predators by virtue of reinforced shells (Vermeij, 1978) or have distasteful tissue (Thayer, 1985), yet *M. edulis* (the common blue mussel) has neither defense. Paradoxically, *M. edulis* flourishes in association with predators, and in sheltered bays in New England, mussels occur with a common predatory gastropod, the dogwhelk *Nucella lapillus.* Dogwhelks readily take mussels and can easily kill them by drilling through the mussel's relatively thin shell (Menge, 1978a, b, 1983; Hughes and Dunkin, 1984).

This study assesses the effectiveness of a novel antipredator defense of *Mytilus edulis* against *Nucella lapillus.* Groups of mussels immobilize dogwhelks with byssal threads, which are secreted by a gland in the mussel's foot and are normally used by the mussel to attach to the surface. This defense by *M. edulis* against predators has been observed on the east coast in response to the presence of the oyster drill *Urosalpinx cinerea* (Carriker, 1981) and on the west coast of North America in response to attacks by *Nucella emarginata* and *N. lamellosa* (Wayne, 1980). Similar responses by

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M. californianus to *N. canaliculata* have been observed on the west coast of North America (T. H. Suchanek, pers. comm.).

Studies with *Mytilus edulis* have been done only in the laboratory. Carriker's (1981) observations were made at 15°C, and *U. cinerea* were inactive at this temperature. Wayne (1980) has documented a series of specific responses by mussels to whelks. Besides attachment of byssal threads, Wayne observed a mussel would open and close its valves and would extend its mantle. The responses were highly stereotyped and occurred only in the presence of *N. lamellosa* and *N. emarginata*. The whelks were assumed to be at risk because they used their radulae to strike at the mussel's foot during attempts to attach a byssus (Wayne, 1980).

However, there has been no assessment of the risk to individual whelks. This report documents the distribution of *N. lapillus* with respect to *M. edulis* and the risk of being trapped by byssal threads under natural conditions.

Materials and Methods

Observations were made between June 1983 and July 1986 just below Mean Low Water (−0.3 to 0.0 MLW) at five sites within protected bays on Swans Island, Maine (44° 10′ N, 68° 25′ W). Four sites (Long Cove, Mill Pond, Mill Pond South, and Mill Pond Point) on the eastern shore of Burnt Coat Harbor, and a fifth site on the eastern shore of Mackerel Cove were used. Long Cove was used only in 1983. Mill Pond South and Mill Pond Point sites were less than 200 m apart; the other sites in Burnt Coat Harbor were 500–1000 m apart. The substratum at all sites was a mixture of granite outcrops, boulders, and cobbles. Barnacles (*Semibalanus balanoides*) and mussels (*Mytilus edulis*) were the most common sessile organisms, and algae covered less than 5% of the surface (see Petraitis, 1987, for a more detailed description of sites).

To document the distribution of *Nucella lapillus* in relation to mussel beds, the amount of surface covered by mussels and the abundance of *N. lapillus* inside and outside mussel beds was estimated. In June 1986, transect lines (88–125 m long) were run parallel to the shore, and the species present were noted at 1 m intervals. On 23–24 June 1986, abundance of *N. lapillus* was sampled with 50 × 50 cm quadrats which were placed outside or inside mussel beds at each site. Mill Pond Point was also sampled on 3 June 1984. Data from the quadrats were bimodal, so Kruskal-Wallis tests (Sokal and Rohlf, 1981), which were corrected for ties, were used to test for differences.

Nucella lapillus that were trapped within mussel beds were tallied over a four year period. At low tide, mussel beds were searched for dogwhelks, and each live dogwhelk was scored as trapped or free. Dogwhelks seen on the margins of the mussel beds were also counted, and some of these individuals were checked for evidence of byssi. No site was surveyed more than once a year.

Two manipulations estimated the rate at which dogwhelks were trapped. In the first experiment, dogwhelks were caged in 15 × 45 × 50 cm baskets for 3 weeks with mussels covering the bottom of the basket. Baskets were made of stainless steel mesh with openings of about 5 × 5 mm. Clumps of mussels were carefully transferred into the cages three to five days before the start of the experiment. On 16 July 1983, three baskets with 25 dogwhelks per basket were started at Long Cove. Between 22 and 23 June 1986, four baskets with 20 dogwhelks per baskets were started at Mackerel Cove, Mill Pond, and Mill Pond Point. Additional treatments with 20 dogwhelk shells per basket or 20 *Littorina littorea* (a herbivorous gastropod commonly found in mussel beds) per basket were used in 1986 to check if mussels were preferentially trapping

TABLE I

Mean number of Nucella lapillus *per 0.25 m² in and out of mussel beds*

	Sampling								
	Within mussel beds				Outside mussel beds				
Location	Mean	S.D.	n	Prop.	Mean	S.D.	n	Prop.	T
Mill Pond South	0.00	0.00	20	1.00	0.15	0.49	20	0.90	2.05
Mill Pond Pt. 84	0.23	0.51	26	0.81	6.03	7.36	29	0.17	25.58
Mill Pond Pt. 86	0.15	0.49	20	0.90	3.26	4.19	19	0.32	14.38
Mill Pond	0.05	0.22	20	0.95	1.90	3.57	20	0.55	8.84
Mackerel Cove	0.05	0.22	20	0.95	0.57	0.75	21	0.57	7.93

n gives the number of quadrats, and prop. is the proportion of quadrats without *N. lapillus*. Column T shows test values for Kruskal-Wallis tests.

live *N. lapillus*. Three baskets of these additional treatments were set out at each site. Data from 1986 were analyzed as a two-way analysis of variance of treatments by sites. The three sites served as blocks, and the analysis was a mixed model with replication. The data, proportions of individuals trapped per cage, were arcsine transformed for the analysis (Johnson and Klotz's transformation, see Sokal and Rohlf, 1981).

The second manipulation was a mark-recapture study. Dogwhelks were marked with red paint and placed in the middle of a mussel bed. On 2 June 1984, 100 marked dogwhelks were released at Mackerel Cove, and individuals were recovered 4 days later. On 24 June 1986, 238 individuals were marked and half were released at Mackerel Cove and half at Mill Pond Point. Recaptures were done three days later. At the same time in 1986, 68 marked empty *Nucella* shells were set in mussel beds at Mackerel Cove and Mill Pond Point to assess the rate at which empty shells were normally trapped and incorporated into mussel beds.

RESULTS

Nucella lapillus were rare in mussel beds, even though mussels were usually the most common sessile organism (Table I, Fig. 1). The overall average density of dogwhelks within mussel beds was 0.10 per 0.25 m^2 while the density outside beds was 2.38 per 0.25 m^2. For each site except Mill Pond South, the difference was significant (Table I). In total, dogwhelks were found in only 12 of the 106 quadrats which were within beds, but in 58 of the 109 quadrats outside beds. The density outside beds is within the range of densities found at these sites at other times (Petraitis, 1987) but below the range of densities reported for more exposed locations (Lubchenco and Menge, 1978).

Just over 27 percent of all live dogwhelks found within beds were tightly bound with byssal threads (average of entries in Table II). Over the four year period, only 293 individuals were found within beds, although 4186 dogwhelks were recorded on the margins of mussel beds. Although each site was searched as nearly as possible with the same amount of effort, the number of dogwhelks seen and trapped varied year to year and site to site (Table II).

Position and number of the byssal threads on the trapped *Nucella lapillus* were very distinctive. The three or four mussels closest to, but not necessarily touching,

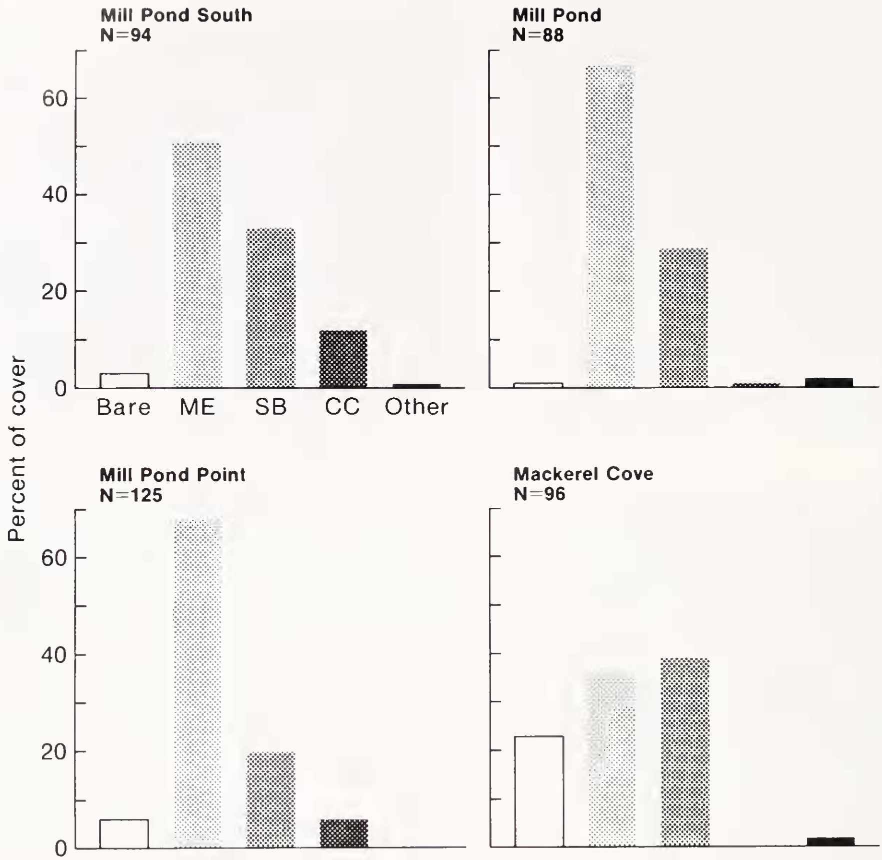

FIGURE 1. Summary of transect data. Abbreviations for species are: ME for *Mytilus edulis*, SB for *Semibalanus balanoides*, CC for *Chondrus crispus*, and OTHER for other algae. N is the number of points sampled.

the dogwhelk attached 20 or more byssal threads to the body whorl of the dogwhelk. The threads appeared to be retracted, flipping the dogwhelk over so its foot did not touch the surface. Dogwhelks were often seen extending the foot in an attempt to right and free itself, although the inverted position and the collective strength of the threads made escape seem unlikely.

Outside mussel beds, the proportion of dogwhelks with remains of byssal threads was highly variable but indicated many encounters between dogwhelks and mussels. From lowest to highest, the proportion of dogwhelks with byssi: 0.05 at Mackerel Cove ($n = 137$), 0.40 at Mill Pond Point ($n = 311$), 0.52 at Mill Pond South ($n = 189$), and 0.75 at Mill Pond ($n = 107$).

There were significant effects of treatment and site in the analysis of variance of the 1986 caging data (Fig. 2). However, only 3% of the total variance was due to differences among the three sites (see Sokal and Rohlf, 1981, for estimation of variance components), and byssal threads were attached more often to live *Nucella lapillus* and empty shells of *N. lapillus* than to *Littorina littorea*. Empty shells were very frequently trapped, but these shells were normally found near the bottom of the mus-

TABLE II

Proportion of live Nucella lapillus *trapped by byssal threads of mussels*

Location	Dates of sampling: 9–14 Jul 1983	4–6 Jun 1984	2–5 Jul 1985	18–26 Jun 1986
Long Cove	0.42 (ND)	ND	ND	ND
Mill Pond S. and Pt.	ND	0.24 (29/842)	0.07 (14/229)	0.52 (64/564)
Mill Pond	0.42 (12/62)	0.16 (25/955)	0.36 (11/491)	0.71 (17/177)
Mackerel Cove	0.00 (47/97)	0.15 (39/149)	0.15 (40/151)	0.25 (8/411)

ND stands for no data. Ratios in parentheses are the total number of live dogwhelks (trapped and free) found in mussel beds over the total number seen in and out of beds while sampling. The proportion is based on the number found in the mussel bed, *e.g.*, for Mill Pond in 1983, 0.42 = 5/12.

sel clump and were attached with very few byssi. In contrast, the live *N. lapillus* which were trapped were usually on the top of the mussel clump and covered with many byssal threads. The low incidence of trapping *L. littorea* may be unrelated to the ability of mussels to distinguish between dogwhelks and periwinkles. Periwinkles are much more mobile than dogwhelks, and thus periwinkles may not be sitting in one spot long enough for a mussel to attach a byssus.

Based on the caging study, the overall per day risk was 0.014 with a quarter of the dogwhelks trapped after three weeks. A dogwhelk had a half-life of 50 days, and an individual had less than a 1 in 5 chance of surviving its active season if it remained within a bed during summer and early fall (about 120 days).

The average per day risk was 0.038 (S.D. = 0.020) for the *Nucella lapillus* in the mark-recapture study (Table III). Dogwhelks were trapped very quickly, and stood a 50:50 chance of being trapped in 2 to 4 weeks. Empty shells of dogwhelks which were marked and placed in mussel beds were also trapped but at a lower rate (Table III). For live *N. lapillus,* the estimates may be high because it was assumed that all unaccounted dogwhelks left the mussel bed. If these individuals remained in the bed but were undiscovered, then the average risk was reduced to 0.010 per day.

Success at finding marked shells and dogwhelks did not differ; in 1986, 75.0% of the empty shells and 70.6% of *N. lapillus* were recovered. A two by two Chi-square test of independence, using data from 1986 in Table III, was not significant ($\chi^2 = 0.85$ with one degree of freedom).

DISCUSSION

Observations and manipulations show that *Nucella lapillus* runs a substantial risk of being immobilized by byssal threads of *Mytilus edulis.* Given the level of risk, one would expect dogwhelks to avoid mussel beds even though mussels are a common prey item of dogwhelks (Menge, 1976; Hughes and Dunkin, 1984). Although sampling confirms this notion (Table I), it is possible that *N. lapillus* are not so much avoiding mussel beds but are searching for an alternative prey, such as the barnacle *Semibalanus balanoides,* outside of the mussel beds. It is also possible that predators

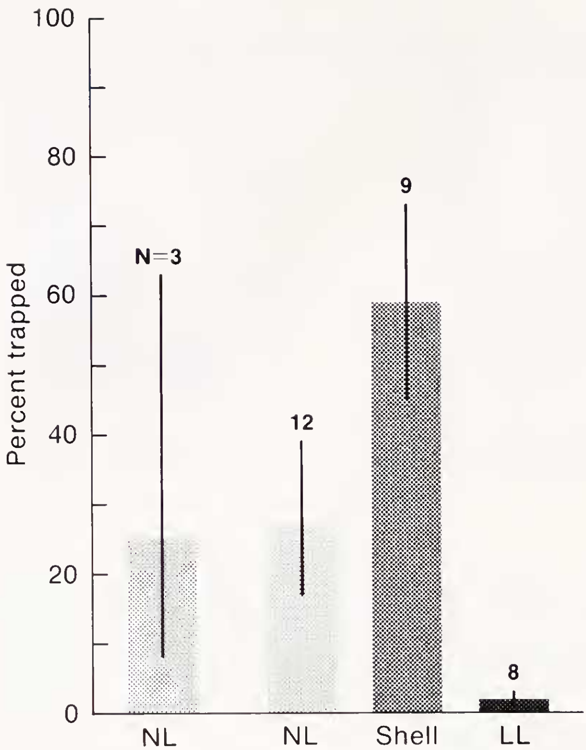

FIGURE 2. Means ± 95% confidence limits with sample sizes (N) for percentage of individuals trapped by byssi in the caging experiments. The leftmost bar gives 1984 data; the rest for data collected in 1986. The treatments are abbreviated as: NL for *Nucella lapillus*, LL for *Littorina littorea*, and SHELL for shells of *Nucella lapillus*. Blocks were ignored in calculating the means and confidence limits for 1986 data; one observation is missing from the LL treatment. Based on analysis of variance of 1986 data, F = 26.77 for the effect of treatments (tested over interaction mean square which is 134.58 and has 4 degrees of freedom) and F = 4.44 for the effect of sites (tested over error mean square which is 60.37 and has 20 degrees of freedom). Main effects are significant at the 5% level, and there is no significant interaction.

quickly remove *N. lapillus* from mussel beds or that mussel beds are an unsuitable habitat for other reasons.

Nevertheless, the rarity of *Nucella lapillus* in mussel beds is striking because mussels cover more than 50% of the surface at all sites except Mackerel Cove (Fig. 1). If the proportion of *N. lapillus* that are outside mussel beds is adjusted for the area covered by mussels, then less than 10% of all dogwhelks are found within mussel beds. For example, at Mackerel Cove 36% of the surface is covered by mussels, and there are 0.05 dogwhelks per 0.25 m^2 within beds and 0.57 dogwhelks per 0.25 m^2 outside mussel beds (see Table I and Fig. 1 for data). Adjusting the densities for the proportion of area occupied by mussels, this means 95% of the dogwhelks are not in mussel beds (*i.e.*, $0.95 = (0.64)(0.57)/[(0.64)(0.57) + (0.36)(0.05)]$).

The behavior of *Nucella lapillus* suggests large individuals of *Mytilus edulis* are dangerous prey. *Nucella lapillus* that have previously taken mussels drill well away from the mussel's foot and byssi, slightly ventral and anterior to the posterior adductor muscle (Hughes and Dunkin, 1984). While Hughes and Dunkin (1984) suggest this position gives the highest caloric return, it is also likely to be the least dangerous.

TABLE III

Mark and recaptures of live individuals and shells of Nucella lapillus

Location	Marked		Recaptures			Risk (#/day)
	Object	n	Trapped	Free	Not in bed	
Mackerel Cove 1984	Snails	100	4	43	4	0.022
Mackerel Cove 1986	Snails	119	10	50	29	0.061
	Shells	68	0	49	0	0.000
Mill Pond Pt. 1986	Snails	119	3	31	45	0.031
	Shells	68	3	50	0	0.019

Column labeled "Not in bed" gives the number found on the margins and outside of the mussel beds. Risk is the exponential rate of trapping.

In addition, these "experienced" *Nucella lapillus* generally prey upon smaller mussels even though they do not provide the highest caloric return (Hughes and Dunkin, 1984), possibly because a small mussel cannot ward off an attack and thus involves less risk.

Cooperative defense by group-living animals is well-known (*e.g.*, Alexander, 1974; Buss, 1981), but its possible importance for sessile non-clonal organisms such as *Mytilus edulis* is not appreciated. Because *Nucella lapillus* is usually immobilized by several mussels, solitary mussels may be much more likely to be taken by *N. lapillus.* Thus mussel beds may provide a common, group protection and may explain the absence of solitary mussels in areas where dogwhelks are common. There are other possibilities. For example, mussels are also the prey of seastars, crabs, fishes, and shore birds (Mason, 1972; Menge, 1976; Edwards *et al.*, 1982; Hughes and Dunkin, 1984; Thayer, 1985), and it may be easier for these predators to remove a solitary mussel rather than one in the midst of a bed.

The behaviors of *Nucella lapillus* and *Mytilus edulis* and the success of *M. edulis* in immobilizing *N. lapillus* suggest byssal threads provide a specific and successful defense against predatory gastropods. It is possible that the mussel's response to predators is an elaboration of a cleaning behavior; *M. edulis* sweeps its shell with its foot preventing fouling by other organisms (Thiesen, 1972). However, the mussel's specific responses to *Nucella* (Wayne, 1980) and the mussel's characteristic placement of byssi on a dogwhelk's shell suggest this is not simply a generalized cleaning behavior. Moreover, the avoidance of mussel beds by dogwhelks (Table I), the use by a dogwhelk of its radula to strike at a mussel's foot (Wayne, 1980), and the positioning of dogwhelks on the valves of mussels (Hughes and Dunkin, 1984) support the notion that the mussel's behavior is a successful defensive action.

While the behavior of *Mytilus edulis* may be adapted as a specific defense against *Nucella,* it is possible other species of mussels could respond to predatory gastropods in the same way. Furthermore, if these behaviors are common, then the absence of a thick, reinforced shells may be a poor indicator of vulnerability to predation.

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